Test of the May Model:
I. Community Ecological Studies of Mushroom Foray Results in the Same and Different Regions

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Abstract

In an effort to test the May Model, standard community ecology analyses were used to examine the data of four forays of Foray Newfoundland and Labrador, three a year apart in the same ecoregion, primarily dominated by boreal forest, and a fourth in a northern coastal ecoregion, dominated by *Empetrum* heath. The first three forays show a species accumulation curve that suggests that a single foray collects very few of the species of the region. Analyses showed high species richness, as well as high species evenness, from all forays. The distribution of the species collected at each foray consisted of a small portion, comprising most of the common species of the region, and a much larger portion of uncommon species. Average overlap of species between any two forays from the same region was 44% of collected species. These findings conform to the May Model.

Key words: May Model; mushroom foray, species diversity, richness, evenness; mycotal ecoregion comparison.

Introduction

The distribution and abundance of fungi may be limited by substrate characteristics, particularly pH, temperature, light and moisture. Other factors that limit fungi include the presence of specific substrates or specific mycorrhizal partners. Consequently, many fungal species are limited to specific habitats, while other species with less demanding requirements thrive equally well in a wide range of habitats. Therefore, each distinct habitat can be expected to have its own distinct mycota, with overlap of species with other habitats because of the ubiquitous presence of more tolerant or pedestrian species. Censuses of fungal communities in larger regional surveys can be expected to have more overlap in species compositions because of shared or overlapping habitats. This suggests that the abundance and diversity of species collected on traditional amateur mushroom forays should remain similar from year to year in the same region and differ from those of any other region, depending on the degree of habitat similarities. However, we know from foray censuses that this is not the case: species overlap is quite low for forays repeatedly carried out in the same or in floristically similar regions (Leacock et al., 1999).

This lack of similarity in foray censuses from the same region may be explained by the May Model (Voitk, 2006), which postulates that forays typically collect only a very small proportion of the mushroom species in any region at one particular time. Mushrooms collected on forays can be assigned to two groups: a small proportion of common species and a larger proportion of less common and rare species. Most of the common species typically are collected at each foray, while the majority of the uncommon and rare species often are not collected at subsequent forays. Thus, species lists from separate forays can differ so dramatically, that using foray census data is limited, if used to differentiate regions.

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Figure 1. Boreal forest of Gros Morne National Park. Boreal forest, barren mountain and fen readily seen. Some Larix laricina *seen silhouetted against sky.* Abies balsamea, Picea glauca, *and* Picea mariana *are the most important conifers.* Betula papyrifera *and* Alnus *spp. make up the majority of leafy trees.*

The purpose of this study was to test the May Model using species diversity and community indices for three consecutive forays conducted in the same ecoregion and one in a separate ecoregion, expected to have limited similarities in community composition. To minimize differences from temporal or seasonal factors, forays were done in the same month (September) and two forays in different ecoregions were conducted within the same week. Four separate forays were conducted in 2003, 2004 and 2005 in Gros Morne National Park (G3, G4, G5) and in 2005 in the Forteau Barrens (L5), Newfoundland and Labrador, Canada. The area foraged in Gros Morne falls within the Serpentine Range Subregion of the Western Newfoundland Forest Ecoregion and the area foraged in Labrador falls within the Forteau Barrens Ecoregion, as defined by the Newfoundland and Labrador Parks and Natural Areas Division document describing the ecoregions of Newfoundland and Labrador (2007).

Materials and Methods

Gros Morne National Park

Gros Morne National Park contains three major vegetation types: highland tundra, boreal forest, and coastal bogs and fens (Berger et al., 1992). The boreal forest in the park area is dominated by balsam fir (*Abies balsamea*). Forest composition and structure (Figure 1) is heavily influenced by insect outbreaks and large-scale windthrow rather than by fire. Other major tree species are white spruce (*Picea glauca*), black spruce (*Picea mariana*), birch (*Betula papyrifera* and *B. cordifolia*), and eastern larch (*Larix laricina*). Bedrock includes serpentinized peridotite in the Tablelands area, limestone around Bonne Bay and on mountaintops and slopes, basalt at Green Gardens and the Gregory Plateau, shales and ribbon limestone ridges along the coastal lowlands, and granite and gneiss in the Long Range highlands. The highlands (reaching an elevation of 800 m) were eroded into a knob and basin terrain during the Pleistocene, and have extensive felsenmeer fields and barren, exposed rock summits. Between the mouths of the glacial troughs are large interlobate moraines. The lowlands are covered with a veneer of marine-washed glacial till of various depths. Extensive bogs and fens have developed in the shale hollows of the coastal lowlands, since the limestone ridges that lie parallel to the coast and the Long Range escarpment impede drainage to the sea. Forest covers about 44% of the park area, wetlands 11%, and tundra 35% (Burzynski et al., 2005).

Human beings have lived in the park area for about 4,500 years, and European settlement began around 1800. Today approximately 3,000 people live in the enclave communities. Commercial forestry in what is now the park began around 1900, and lasted until park establishment in 1973. As part of the Federal-Provincial Agreement for the establishment of Gros Morne National Park, the park maintains 12 domestic tree harvest blocks for the use of local residents. Over the years, much of the accessible forest has

Figure 2. Empetrum *barrens of Labrador Straits. Typical heath plants and dwarfed trees. Forests of taller trees only in protected river valleys.*

been utilized for domestic purposes such as boat construction, home building, and heating, but such activities have had minimal effects on Park forest beyond the communities.

Labrador

Low *Empetrum* heath grows on headlands along the coast of the Labrador Straits area, between Blanc Sablon (Québec) and Red Bay (Newfoundland and Labrador). Inland from the shore is a tangled dwarfed coastal krummholz forest (locally called "tuckamore") of white spruce and balsam fir (Figure 2). Highlands are covered in rock barrens or *Empetrum* heath, and small trees are restricted to sheltered locations. Larger valleys are densely forested.

Cambrian and Late Proterozoic sandstone, basalt, and limestone in the south, and Middle Proterozoic granite in the north, underlie the coast of the Labrador Straits (Coleman-Sadd et al., 1994). The whole area was heavily glaciated during the Pleistocene, and the hills are generally flat-topped and low. Deep till deposits fill some low-lying areas, and sand dunes extend along the shore at L'Anse Amour and the mouth of the Pinware River. Labrador has been populated, albeit sparsely, for about 9,000 years.

Traditional forays with approximately 45 participants each were held over a fall weekend; participants divided into small groups, each with a leader, collected specimens along designated trails. With each collection records were made for location, habitat, substrate, collection date, collector and identifier. The volunteers attempted to sort and identify specimens, but appointed experts authenticated all identifications, with the aid of standard chemicals, dissecting and compound microscopes, a reasonable library of reference literature and collegial consultation. After 2003, all identified specimens were photographed, and voucher specimens were dried and stored in the Herbarium of Gros Morne National Park. A database was developed from the collecting slips and reconciled for the annual species list. The annotated cumula-

tive species list, annual lists, and reports may be downloaded from www. nlmushrooms@.ca, the Web site of Foray Newfoundland & Labrador.

Only mushrooms identified to species have been considered in this study. In all three of the Gros Morne forays, frequency of occurrence was not recorded for some identified species. Those species were omitted from calculations in which frequency is required. The full list of identified species was used for analyses in which frequency is not required. A species was considered to be *common* if the number of collections of that species was more than the mean plus two standard deviations of the number of collections of all species for the foray. Species were considered *consistent* if they were collected each year of the three Gros Morne forays, regardless of their abundance.

The following community indices were used to assess the mushroom communities sampled from the four forays: Simpson's Index of Diversity to measure the diversity (dominance) of the foray lists, Shannon-Wiener index to measure species heterogeneity (a check for evenness) and Sørensen's coefficient to assesses species overlap between forays. Please refer to Appendix A for more detailed explanations and equations for these tests.
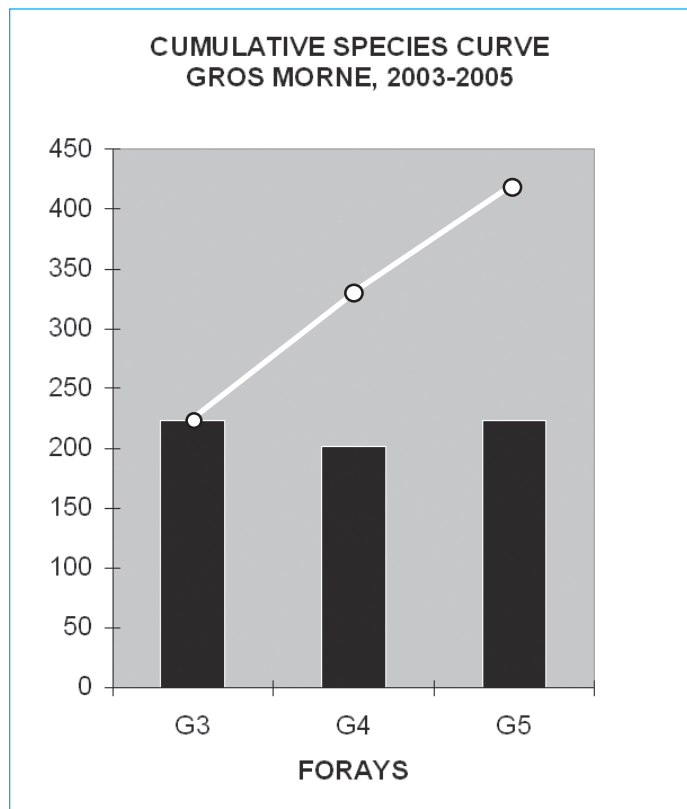
Results

Approximately 200 species were recovered in each foray, yet differences in the species collected led to a steadily rising cumulative species curve, which gives no sign of leveling off (Figure 3). Figure 4 shows the curves for the number of collections and species for all forays. Of the approximately 200 species collected at each foray, fewer than 20% were common by our definition. Over 75% of common species were also consistent species (collected each year). Table 1 shows the actual number of species identified at each foray (R1), the number for which frequency was recorded (R2), Simpson's Index of Diversity (SID) and Shannon-Wiener Index of Diversity (SWI) for each foray. Simpson's Index of Diversity was consistently high for all forays, although slightly lower for the Labrador foray than the three Gros Morne forays. The Shannon-Wiener Index of Diversity was very high for all forays. The results for Sørensen's coefficient are shown in Table 2. The average overlap of common species between any two Gros Morne forays was 44%. Comparing the Labrador foray with any Gros Morne foray showed an average overlap of 29%.

Figure 3. *Number of species collected during each Gros Morne foray (black bar) and their cumulative species curve (white line). The steady ascent of the cumulative species curve, without sign of leveling off, suggests that 417 is nowhere near the total number of species in the Gros Morne area surveyed.*

Table 1
Community analyses for all forays. (See text for explanation). R1 is total number of species, while R2 is total number of species for which frequency was recorded. SID = Simpson's Index of Diversity, SWI = Shannon-Wiener Index of Diversity.

FORAY	R1	R2	SID	SWI
Gros Morne 2003	223	171	0.9907	4.9028
Gros Morne 2004	202	191	0.9905	4.9483
Gros Morne 2005	223	205	0.9925	4.5068
Labrador 2005	148	148	0.9839	4.5590

Table 2
Sørensen's Coefficient of Similarity: percent of mushroom species common to any two forays.

	G3	G4	G5	L5
G3	100			
G4	39.06	100		
G5	43.05	49.41	100	
L5	32.35	25.71	28.57	100

Discussion

The May Model postulates that for mushroom forays in regions comprised of multiple habitats:

1. A foray collects only a very small portion of all the species in its region.

2. Species collected at a foray divide into a small group of common mushrooms and a considerably larger group of mushrooms unlikely to be found again, with a gradual or even progression from one extreme to the other, i. e. much species diversity (high richness) with little dominance (high evenness).

3. A foray collects virtually all the common species in its area but only a small proportion of the uncommon mushrooms.

4. With respect to similarity or overlap of species collected, forays conducted in one region during different years differ markedly from each other.
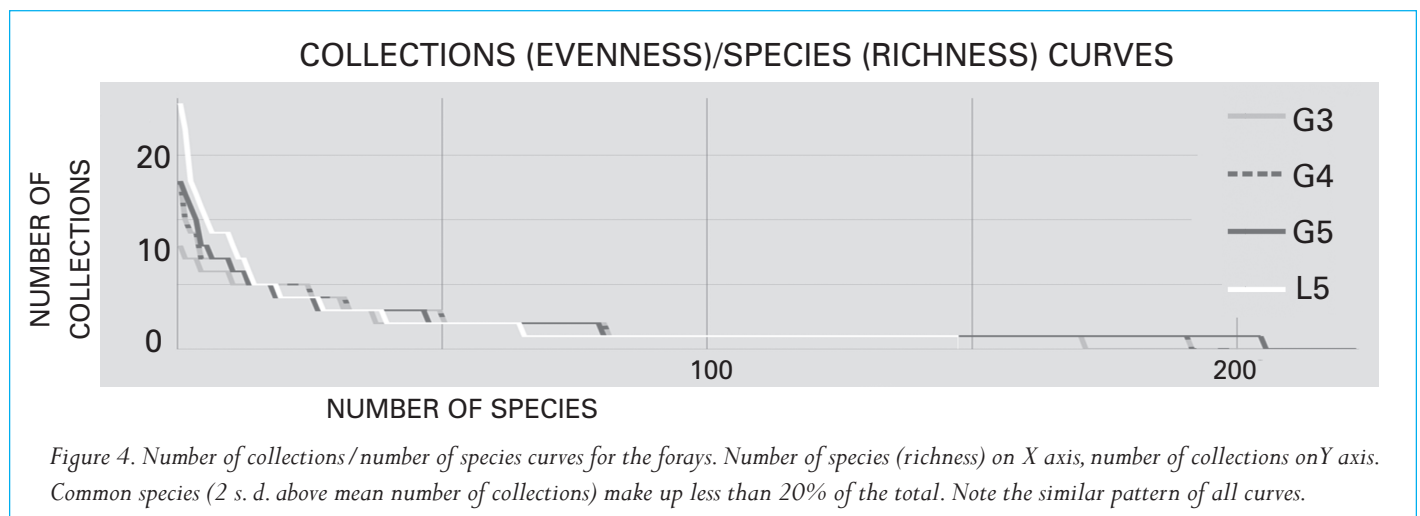
Thus, according to the May Model, studies of species richness and evenness should be similar for forays in regions comprised of multiple habitats and species similarity or overlap should be relatively small from year to year within one region.

Our finding of a relatively stable and high number of species each foray, together with a steadily rising cumulative species curve (Figure 3) supports the May Model concept that the region contains many more species than were collected at any foray or have been collected cumulatively to date. This experience is not unique to our forays, of which only three were in the same region. Others have reported a similar curve, some with over 20 years of forays in the same region (Tofts and Orton, 1998; Straatsma et al., 2001; Roberts et al., 2004; Kendrick, 2005). The North American Mycological Association, foraging the much larger region of North America, reports a similar curve for 42 forays (Leacock, 2007). Our number of collections and species curves (Figure 4) are a graphic representation of species diversity and dominance, showing high diversity (many species) and low dominance (collections of no species overwhelmingly dominating the group). Note that the curves of all forays are very similar in this regard. These data also show that uncommon species make up the bulk of species collected at a foray, accounting for more than 80% of all collected species. This is consistent with the May Model. Over 75% of these common species are also constant species, suggesting a close relationship between these two parameters.

The high values seen in the Simpson's Index of Diversity indicate that the species diversity of the communities was very high—two randomly selected individuals would be unlikely to belong to the same species. The values found using the Shannon-Wiener Index of Diversity suggests that in each foray the mushroom communities had a great number of species with an even distribution. These observations for both the Simpson's Indices and the Shannon-Wiener Index were similar for the Gros Morne forays and the Labrador foray: a high mushroom diversity with little variation and very few dominant species. In other words, these indices showed that there were very few common mushroom species (species with many collections, i. e. dominant species) and a large number of uncommon species (species with few collections), a pattern denoting species evenness. These findings again conform to the May Model.

Our findings using Sørensen's Coefficient confirmed that the Gros Morne forays differed from each other by a consistently high number of different species each time; only 44% of species were common from one year to the next. Our finding that the three Gros Morne forays differed considerably from each other is not unique. For example, Leacock et al. (1999), reviewing NAMA foray records, report that "surprisingly" the overlap between three forays in Minnesota and five forays in Michigan was only 30%, "even though they are in the same Great Lakes floristic region." According to the May Model, both Leacock and associates' and our observations are expected rather than surprising: a small proportion of the total species is collected by any foray, made up mostly of uncommon species, causing species lists to differ from foray to foray in the same region.

Figure 4. Number of collections/number of species curves for the forays. Number of species (richness) on X axis, number of collections on Y axis. Common species (2 s. d. above mean number of collections) make up less than 20% of the total. Note the similar pattern of all curves.

Community ecological analyses presume that the samples taken adequately represent their communities. Mushroom forays collect a portion of all the species in the region that may be too small in relation to the entire mushroom community in that region, to be an adequate representative of that community. This is probably because the whole organisms, fungi with their extensive mycelial network, are not readily visible and they are usually sampled by collecting only their visible fruiting bodies, mushrooms. However, because fungi vary considerably in the frequency of their fruiting, fruiting body sampling recovers a very small segment of the fungal community each time, and that segment differs significantly from one year to the next. Therefore, foray samples may be inadequate representations of their mycological communities, making community ecological analyses somewhat ineffective assessment tools.

The May Model is an untested theoretical concept. This communication is a first attempt to test some of its contentions, using data from our own forays. Although our results suggest that the May Model is robust on initial examination, our data are limited and, at best, this study should be considered a preliminary report. Therefore, we invite other workers, especially those with long-standing forays and much larger data sets, to analyze their results for a more reliable assessment of the May Model.

Appendix A
Explanations and equations of statistical tests used

Simpson's Index of Diversity

Simpson's Index of Diversity relates the number of species (species richness) to the proportion of each species from a biodiversity sample within a local community such as a mushroom foray (Brower and Zar, 1984). The index evaluates whether the community is dominated by a limited number of common species. The value of the index ranges from 0-1, where 1 represents maximum species diversity and 0 indicates complete dominance by a single species (Krebs, 1999). It is calculated as Simpson's $(D) = 1 - "(Pi2)$; Pi is the proportion of the total number of individuals represented by species i and is calculated as $Pi = n/N$, where n is the number of individuals for a particular species and N is total number of species in that community.

Shannon-Wiener Index of Diversity

The Shannon-Wiener Index of Diversity measures the number and proportion of each species within a local community (Brower and Zar, 1984). The index is maximized if the community has a large number of species with numbers of individuals equitably divided amongst species i. e. high species evenness (Krebs 1999). The calculation for Shannon-Wiener Index of Diversity (H) is: $(H) = -"(Piln[Pi])$.

Sørensen's Coefficient of Similarity

Sørensen's Coefficient of Similarity assesses the percent similarity in species composition between two communities, taking into account the total number of species found and the number of species common to both communities. Its calculation is as follows: $CCs = 2c/(s1 + s2)$, where CC is the Community Coefficient, c is the number of species in common between the 2 communities, and s1 and s2 are the number of species in communities 1 and 2, respectively (Krebs, 1999).

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